

# UTILITY OF GROWTH RINGS IN THE AGE DETERMINATION OF CHAPARRAL SHRUBS

JON E. KEELEY

Department of Biology, Occidental College,  
Los Angeles, CA 90041

## ABSTRACT

Use of plant growth rings for age determination requires distinct rings and verification that these are produced annually. In this study of southern California chaparral shrubs, the sharpest rings were produced by shallow-rooted, non-sprouting species of *Arctostaphylos* and *Ceanothus*. The least distinct rings were produced by the deep-rooted resprouting shrub *Malosma laurina*. Ring counts on stems from stands of known age indicated that on some sites the majority of shrubs can be accurate indicators of stand age; but, some may not be. Non-sprouting species of *Ceanothus* and *Arctostaphylos* were good indicators of stand age as stems generally did not deviate from stand age by more than 5%. However, in older stands a large proportion of these taxa could not be aged due to heartrot. Some stems on resprouting shrubs deviated widely from stand age. Interpretation of this pattern is complicated by the often continuous nature of stem recruitment in years subsequent to fire and thus, many of the stems (ramets) of such species will not be an accurate measure of the shrub (genet) age. At one site, an indirect technique was used to show that shrubs are not producing extra "false rings" or are not missing rings. At this site there was a marked synchrony of maximum ring width for the same year for six species. This ring was the widest, out of the last 16 rings, and coincided with one of the highest rainfall years in recent history.

Growth rings have proven to be an invaluable resource for age determination in woody plants. The technique requires the presence of growth rings with a clear demarcation between spring wood and summer wood and the verification that these are produced annually. Studies in the southwestern U.S. have verified the annual nature of growth rings in trees and shrubs of some species (Stokes and Smiley 1968; Ferguson 1959, 1964; Roughton 1972; Arno and Wilson 1986). However, the technique does not work well on all species or all individuals of a species; some do not produce discernable growth rings and others, with distinct growth rings, do not reliably produce a single ring annually (e.g., Ferguson 1959; Roughton 1972; Carlquist 1980).

Most chaparral shrubs produce a growth ring in which spring and summer wood are distinguishable (Webber 1936; Watkins 1939; Fishbeck and Kummerow 1977; Carlquist 1980; Kummerow et al. 1981; Michener 1981). Species differ, however, in being ring porous or diffuse porous, in the cells which produce the ring pattern and the distinctness in the ring boundary. Several studies of chaparral have used growth rings to determine age (Sampson 1944; Hedrick

1951; Patric and Hanes 1964; Stocking 1962; Keeley 1975; Guntle 1974; Schlesinger and Gill 1978; Kummerow et al. 1981; Hubbard 1986; Montygierd-Loyba and Keeley 1986) although verification of their annual nature has usually been lacking. Due to the seasonal growth conditions imposed by the mediterranean climate, the assumption of annual ring deposition seems justifiable. Verification, however, is the *sine qua non* for accurate age determination by ring counts because two growth anomalies are possible (Fritts and Swetnam 1989). In years of extremely low rainfall, cambial growth may be limited to the extent that a growth ring will not be laid down. Failure to recognize such "missing rings" will underestimate the age of a stem. In some years, renewed growing conditions near the end of the growing season can result in an additional spurt of growth and laying down of an additional "false ring." Failure to recognize false rings will overestimate the age of a stem.

The purpose of this study was to determine which chaparral species produce discernable growth rings and evaluate to what extent they could reliably be called annual rings. Two approaches were taken. One was to determine the age of the largest stem on chaparral shrubs from sites of "known" age. The other part of this study was to evaluate an indirect measure of the extent of false or missing rings. Ring width, which often reflects climatic favorableness, was measured on the dominant shrubs for each of the last 16 rings. If rings are faithfully laid down each year there should be a degree of synchrony in growth ring width among species that is correlated with climatic conditions, in particular, precipitation.

#### STUDY SITES AND METHODS

For the first part of this study, stands of known age were selected from fire maps produced by the Los Angeles County Fire Department, Forestry Division, the USDA Forest Service, Angeles National Forest and historical records in Minnich (1987). Due to the large scale at which such maps are made, and the potential for wildfires to leave unburned islands of vegetation within their boundaries, this technique of ascribing stand age carries with it some potential for error.

Five sites, of 9, 24, 28, 65 and 88 years of age at the time of sampling (fall 1984), were selected. The locations were as follows: 1) The Clear Creek Fire burned in 1975 in the San Gabriel Mtns (Los Angeles Co.) near the Clear Creek Forestry Station. Plants were sampled N of Angeles Crest Hwy at the Clear Creek Overlook (1100 m). 2) The Johnstone Fire burned much of the San Dimas Experimental Forest (Los Angeles Co.) in the San Gabriel Mtns in 1960. Plants were sampled above Bell Canyon (800 m). 3) The Sherwin Fire burned an extensive portion of the western end of the Santa

Monica Mtns (Ventura Co.) in 1956. Shrubs were sampled along Yerba Buena Rd (600 m). 4) The San Gabriel Fire burned much of the San Gabriel Mtns (Los Angeles Co.) along the Glendora Mtn Rd. and Glendora Ridge Rd. in 1919. Plants were sampled near the junction of those two roads (975 m). 5) In 1896 a massive fire burned most of the chaparral along the Angeles Forest Highway (Los Angeles Co.). Although much of the area burned again in the early 1980's, a pocket of vegetation was untouched and this site, ½ km N of the Monte Cristo Ranger Station (1000 m), was sampled.

In the field a stem section of several cm thickness was cut at ground level. Depending upon the community composition, two to six species were sampled from each site. For each species five or more shrubs were sampled. Many plants had more than a single stem and on these the largest stem was sampled. In the lab, stem sections were polished with high grade (200–300 grit) sandpaper on a belt sander. To make growth rings more readily distinguishable, various techniques were utilized that accentuated the spring wood from the summer wood. These included applying one of the following: water, linseed oil, kerosine or paraffin oil. Distinguishing growth rings on some species, e.g., *Adenostoma fasciculatum*, was sometimes difficult due to dark coloration of the heartwood. Soaking overnight in 5.25% sodium hypochlorite solution bleached out this color. Growth rings were counted under a dissecting microscope at 7–10× power by two independent observers.

The site for the second part of this study was in Silverado Canyon in the Santa Ana Mtns (Orange Co.) at 950 m. According to USDA Forest Service, Cleveland National Forest records, no fire had ever been recorded from this site. Stem sections were collected in fall 1983 from all of the dominant species and treated as described above. Ring width was measured for the last 16 rings on each stem with a micrometer. If these rings were laid down annually, this time period would have included exceptionally wet and exceptionally dry years (data from NOAA 1968–1984).

Nomenclature is according to Munz (1959) except for *Malosma laurina* (Nutt.) Nutt. ex Abrams. (*Rhus laurina* Nutt.).

## RESULTS

The following shrubs produced recognizable growth rings: *Adenostoma fasciculatum*, *Arctostaphylos glauca*, *Ceanothus* spp., *Cercocarpus betuloides*, *Garrya veatchii*, *Heteromeles arbutifolia*, *Prunus ilicifolia*, *Quercus dumosa*, and *Rhamnus crocea* ssp. *ilicifolia*. Some species with diffuse porous wood had less distinct boundaries between rings, making counts difficult and the most difficult were *Rhus ovata* and *Malosma laurina*. *Quercus dumosa* was confusing at first because bands of parenchyma cells were often laid down in waves





FIG. 1. Cross section of *Ceanothus megacarpus* stem illustrating distinct annual growth rings.

during the growing season. Summer wood was, however, characterized by the production of a dense layer of narrow vessels.

One characteristic that separated all of these taxa was the sharpness of the boundary between the spring and summer wood. The most distinct growth rings were produced by obligate-seeding taxa of *Ceanothus* (Fig. 1) and *Arctostaphylos*.

One approach to verifying that growth rings were produced annually was to examine ring counts on stems from stands with known fire history (Table 1). At each site there were some shrubs with ages reflecting the time since the last fire. Shrubs deviating from this pattern need to be evaluated carefully. Deviation from stand age may be due to missing or extra rings, or due to recruitment of stems in years subsequent to fire. The latter factor may be very significant for postfire resprouting taxa, e.g., *Adenostoma*, *Cercocarpus*, *Garrya*, *Heteromeles*, *Quercus*, *Prunus*, and *Rhamnus*. Although the term resprouting derives from the fact that they regenerate vegetatively from the rootcrown after fire, these shrubs are capable of continuous recruitment of stems during the fire-free period. This is illustrated by the age structure of all stems on a single *Adenostoma fasciculatum* shrub (Fig. 2); plant #1 had several stems that date back to near the time of the last fire and apparently stems have established every few years since that time.

Non-sprouting species of *Ceanothus* and *Arctostaphylos* do not

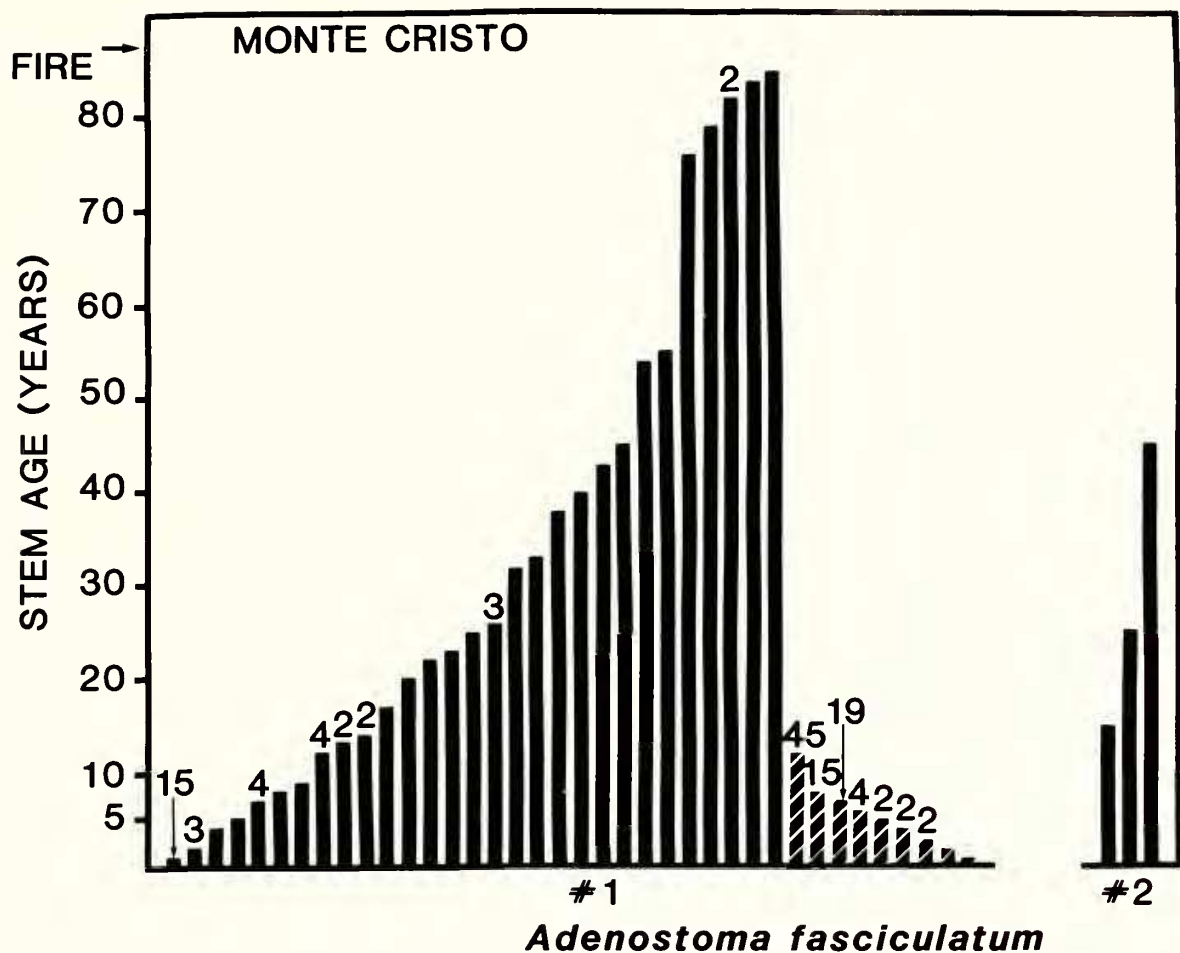


FIG. 2. Age distribution of all stems on two *Adenostoma fasciculatum* shrubs from the Monte Cristo Site. Each solid bar represents one live stem; a number above the bar signifies more than one stem. Cross-hatched bars represent dead stems.

regenerate vegetatively and thus, in the absence of seedling recruitment between fires, all stems should be seen to date back to the time of the last fire, assuming of course that the heartwood is not rotted. There was only one exception (at the Sherwin Site) to the generalization that deviations from stand age were  $\leq 5\%$  for these non-sprouting taxa.

Another approach used to verify the annual deposition of growth rings was to look for synchrony in growth response between plants at the same site. In exceptionally wet years, very wide growth rings are laid down and in exceptionally dry years very narrow rings are produced. If such a 'finger-print' is synchronous among a significant number of plants at a site it is taken as evidence that growth rings are responding to the same annual variations in climate and reflecting annual growth rings. At the Silverado Site the ring width was measured for the last 16 growth rings on stems of six species. Although annual ring width over the entire 16 years was not highly synchronized between plants (data not shown), one extremely good year and several bad years were synchronized between different species at the site (Table 2). For 23 of the 24 stems examined, the 15th

TABLE 1. NUMBER OF GROWTH RINGS ON THE LARGEST STEM FROM SEPARATE SHRUBS COLLECTED IN THE FALL OF 1984 FROM SITES WITH KNOWN FIRE HISTORY. Postfire mode of regeneration; OR = obligate resprouter, FS = facultative seeder, OS = obligate seeder.

Species	Post-fire mode*	% of shrubs dated to last fire		Shrubs deviating from stand age		
		%	(n)	Number of shrubs	Number of growth rings	% deviation from stand age
Clear Creek Fire (Burned 1975)						
<i>Quercus dumosa</i>	OR	100	(5)	0		
<i>Cercocarpus betuloides</i>	OR	40	(5)	3	8	-11
Johnstone Fire (Burned 1960)						
<i>Ceanothus crassifolius</i>	OS	80	(5)	1	23	-4
<i>Quercus dumosa</i>	OR	60	(5)	2	23	-4
Sherwin Fire (Burned 1956)						
<i>Ceanothus crassifolius</i>	OS	60	(10)	2	29	+4
				1	27	-4
				1	15	-46
<i>Adenostoma fasciculatum</i>	FS	0	(22)	9	27	-4
				6	26	-7
				4	25	-11
				3	24	-14
San Gabriel Fire (Burned 1919)						
<i>Ceanothus crassifolius</i>	OS	80	(5)	1	44 (heartrot)	-
				1	64	-2
<i>Arctostaphylos glauca</i>	OS	40	(5)	1	60 (heartrot)	-
				1	56 (heartrot)	-
				0		
<i>Heteromeles arbutifolia</i>	OR	100	(2)	0		
<i>Adenostoma fasciculatum</i>	FS	33	(6)	1	62 (heartrot)	-
				2	49	-25
				1	36	-45
<i>Garrya veatchii</i>	OR?	0	(1)	1	29	-55
<i>Prunus ilicifolia</i>	OR	0	(1)	1	54	-17
Monte Cristo (Burned 1896)						
<i>Arctostaphylos glauca</i>	OS	33	(6)	1	86	-2
				1	84	-5
				1	69 (heartrot)	-
				1	62 (heartrot)	-
				1	69 (heartrot)	-
<i>Ceanothus crassifolius</i>	OS	0	(6)	1	78 (heartrot)	-
				1	77 (heartrot)	-
				1	71 (heartrot)	-
				1	64 (heartrot)	-
				1	59 (heartrot)	-
				1	51 (heartrot)	-



TABLE 1. CONTINUED.

Species	Post-fire mode*	% of shrubs dated to last fire		Shrubs deviating from stand age		
		%	(n)	Number of shrubs	Number of growth rings	% deviation from stand age
<i>Adenostoma fasciculatum</i>	FS	0	(5)	1	85 (heartrot)	—
				1	84	-5
				1	75	-15
				1	54 (heartrot)	—
				1	45	-49

ring (from the perimeter) was the widest, and in all but one case it was followed by a year with a significantly narrow ring. Ring 15 would have been laid down in the very wet winter and spring of 1969 (precipitation for January, February and March was 224% above normal for the nearest station at Santa Ana). The following year had a very narrow band, as did 1972 and 1981, and these years had 52%, 48% and 60%, respectively, of the average rainfall.

#### DISCUSSION

Rings with a clear demarcation between spring and summer wood are evident in the obligate-seeding species of *Arctostaphylos* and *Ceanothus* (Fig. 1). These non-sprouting taxa have relatively shallow root systems, dating back to establishment as seedlings after the last fire, and consequently are exposed to much lower soil water potentials during the summer drought than are sprouting species (Miller and Poole 1979; Barnes 1979; Schlesinger and Gill 1980; Parsons et al. 1981). In non-sprouting species, stomatal closure may persist for months (Poole et al. 1981), resulting in a sharp cessation in cambial growth and deposition of very narrow vessels (Carlquist 1980). The only report of obscure boundaries between growth rings in obligate-seeding taxa is for two *Arctostaphylos* species from southeastern Arizona (Harlan 1977). The presence of substantial summer rains in that region may account for the difference in distinctness of growth rings from that observed for southern California taxa.

Shrubs with deeper roots sometimes have less distinct rings and this may be tied to the continuation of cambial growth through the summer as observed for *Rhus ovata* (Avila et al. 1975). In the present study growth rings were visible, although not always distinct in *Rhus*. *Malosma laurina* produced the least discernable growth ring, due to its diffuse porous wood (Young 1974). Watkins (1939) noted that annual rings were poorly defined in young twigs of *Adenostoma fasciculatum* and *Prunus ilicifolia*. Observations made in the present study do not concur, and other investigators have reported distinct

TABLE 2. RELATIVE RING WIDTHS FOR SELECTED YEARS FROM 1968 TO 1983 FOR SPECIES CUT IN FALL 1983 FROM THE SILVERADO SITE. For each stem, ring widths were measured and normalized to the widest ring width observed across the last 16 years of rings. Years 1968-1970 are underlined to emphasize the synchrony in growth observed between species.

Species	Stem age	Relative ring width										
		1968	1969	1970	1971	1972	...	1981	1982	1983		
<i>Adenostoma fasciculatum</i>												
#1	(41 yr)	42	<u>100</u>	<u>25</u>	33	16	...	16	33	16		
#2	(41 yr)	54	<u>100</u>	<u>23</u>	31	69	...	15	38	23		
#3	(32 yr)	60	70	30	30	15	...	20	70	70		
#4	(41 yr)	75	<u>100</u>	<u>38</u>	38	50	...	13	38	25		
#5	(54 yr)	81	<u>100</u>	<u>100</u>	36	36	...	27	46	46		
#6	(47 yr)	57	<u>100</u>	<u>29</u>	57	14	...	29	31	38		
<i>Quercus dumosa</i>												
#1	(100 yr)	62	<u>100</u>	<u>46</u>	85	85	...	23	31	38		
<i>Ceanothus crassifolius</i>												
#1	(117 yr)	60	<u>100</u>	<u>20</u>	50	10	...	30	50	10		
<i>Rhamnus crocea</i>												
#1	(117 yr)	18	<u>100</u>	<u>20</u>	50	10	...	30	50	10		
#2	(88 yr)	20	<u>100</u>	<u>33</u>	33	22	...	11	56	78		
#3	(53 yr)	44	<u>100</u>	<u>33</u>	13	13	...	20	13	13		
#4	(59 yr)	20	<u>100</u>	<u>21</u>	21	21	...	21	14	43		



TABLE 2. CONTINUED.

Species	Stem age	Relative ring width										
		1968	1969	1970	1971	1972	...	1981	1982	1983		
<i>Heteromeles arbutifolia</i>												
#1	(100 yr)	42	100	17	8	25	...	33	17	42		
#2	(51 yr)	25	100	13	6	50	...	13	50	75		
#3	(106 yr)	60	100	40	6	6	...	6	20	20		
#4	(55 yr)	50	100	25	50	75	...	38	25	25		
#5	(86 yr)	60	100	70	60	80	...	30	20	20		
#6	(83 yr)	83	100	33	17	50	...	17	17	17		
<i>Rhus ovata</i>												
#1	(57 yr)	40	100	10	20	40	...	30	40	30		
#2	(43 yr)	36	100	54	73	18	...	27	27	27		
#3	(73 yr)	71	100	71	71	71	...	57	57	86		
#4	(43 yr)	57	100	57	29	14	...	43	71	86		
#5	(69 yr)	36	100	9	18	9	...	27	36	46		
#6	(61 yr)	21	100	29	29	21	...	21	29	21		

growth rings in *A. fasciculatum* (Sampson 1944; Stocking 1962; Kummerow et al. 1981).

Studies of the southern Californian chaparral tree *Pseudotsuga macrocarpa* have revealed that absent rings comprised less than 1% of the total rings and false rings were virtually absent (Schulman 1947; Michaelsen et al. 1987). The lack of false rings was attributed to the absence of summer precipitation and, based on ring counts of chaparral stems from stands with known fire history (Table 1), false rings are apparently uncommon in chaparral shrubs; two *Ceanothus crassifolius* at the Sherwin Site did have an "extra" ring each (Table 1). Missing rings, however, might be expected to be more common because the shallow root systems of chaparral shrubs would make cambial growth very sensitive to dry years (Kummerow et al. 1981). Data from Table 1 suggest that for non-sprouting *Ceanothus* and *Arctostaphylos*, missing rings may result in a few percent error when assigning ages based on ring counts.

Interpreting data from Table 1 for sprouting taxa such as *Adenostoma* is more complicated. Some stems give ring counts close to the age of the stand (based on known fire history) but some have many fewer rings. This could be due to a high frequency of missing rings or these stems may have been produced in years subsequent to the fire. The latter is certainly true for many of the stems on resprouting shrubs (e.g., plant #1, Fig. 2). The pattern illustrated by plant #2 (Fig. 2) requires careful analysis. No stem on the plant dates back to within 44 years of the last fire. Three hypotheses could account for this pattern: 1) This plant established from seed 44 years after the last fire, 2) stems initiated after the last fire have died and fallen from the plant, or 3) this shrub has been highly suppressed and is missing many growth rings. The first hypothesis is unlikely since this species has not been observed to successfully recruit seedlings under the canopy of mature chaparral (Keeley 1992); however, an occasional seedling recruited in canopy gaps cannot be ruled out. Based on the generally slow rates of wood decomposition in chaparral (Gray and Schlesinger 1981), the second hypothesis also seems unlikely. Consistent with the third hypothesis is the fact that plant #2 was smaller in stature and seemingly less vigorous than surrounding shrubs. Future research needs to determine the extent to which suppression by competitors may suppress growth and thus suppress annual ring deposition in chaparral shrubs.

One seemingly anomalous growth ring pattern observed in another study (Keeley 1992) was the presence in an *Adenostoma sparsifolium* stem of 40 more growth rings than observed in any other species at the site; two *Ceanothus greggii* and one *Adenostoma fasciculatum* had maximum ages of 65 yr, whereas one *A. sparsifolium* had a stem that dated back 105 yr. This plant, however, apparently survived the last fire at the site and in fact had a very distinct fire scar 40 yr



FIG. 3. Cross section of *Adenostoma sparsifolium* stem aged at 105 yr. Arrow indicates a fire scar at 65 yr of age, which is the maximum age of all other stems counted at the site (Keeley 1992).

earlier (Fig. 3). Such fire scars are common in conifers but are not expected in chaparral shrubs since it is rare for a shrub to survive a wildfire. The arborescent nature of *A. sparsifolium* and the more open nature of the interior chaparral site where this plant came from may account for this unique phenomenon (Fig. 3).

A technique often of use in evaluating the extent of missing or false rings is called "cross-dating" (Stokes and Smiley 1968; Fritts and Swetnam 1989). It is based on two principles: 1) annual variations in climate (predominantly precipitation in the southwest) are reflected in variation in ring width, i.e., a year of high rainfall produces a wide growth ring whereas a year of low rainfall produces a narrow ring, and 2) there is a synchrony between different trees in a locality or region. After examining sequences of good and bad years for a substantial number of trees, a master chronology is developed to which all ring chronologies in a region are compared. For any particular site, deviations in alignment (with the master chronology) of good or bad years is accounted for by either taking out presumed 'false' rings or adding presumed 'missing' rings.

A priori one might predict chaparral shrubs would not be readily amenable to cross-dating. Based on extensive dendrochronology studies, it is commonly accepted that cross-dating is not likely to be successful on sites where plants are in close competition, as this



may override climatic signals (Glock 1937, Stokes and Smiley 1968). Competitive effects are likely a dominant factor controlling growth of chaparral shrubs (Schlesinger and Gill 1978, 1980). Substrate may also influence synchrony of growth response. In chaparral, marked heterogeneity in subsurface topography results in much diversity in rooting depths from one microsite to another (Kummerow 1981). This is likely to produce very different water relations between plants in the same community, even within the same species (Schlesinger and Gill 1980) and thus different growth responses. Another factor making cross-dating less feasible in shrubs is the shorter lifespan which provides fewer rings for matching. One attempt to cross-date shrubs from two sites in this study with a known regional chronology (developed by The Laboratory of Tree Ring Research, University of Arizona) produced equivocal results (Keeley unpublished data). However, the demonstration of marked synchrony to the extremely wet year of 1968 at the Silverado Site (Table 2) lends support to the conclusion that these shrubs do lay down annual rings and that the missing rings introduce a relatively small error.

In summary, there is good evidence that for many shrubs growth rings give a close approximation of age, although in general it would be premature to place high confidence in assigning precise years to most rings. Comparisons with stands of known age suggest that for the non-sprouting species of *Ceanothus* and *Arctostaphylos* there may be  $\leq 5\%$  error. The observation of ring counts for *Adenostoma fasciculatum* indicate the possibility that the error is greater, however, since resprouts can be initiated in years subsequent to the first postfire season, the deviation from stand age may be a function of recent recruitment and not due to missing rings.

#### LITERATURE CITED

- ARNO, S. F. and A. E. WILSON. 1986. Dating past fires in curleaf mountain-mahogany communities. *Journal of Range Management* 39:241–243.
- AVILA, G., M. LAJARO, S. ARAYA, G. MONTENEGRO, and J. KUMMEROW. 1975. The seasonal cambium activity of Chilean and Californian shrubs. *American Journal of Botany* 62:473–478.
- BARNES, F. S. 1979. Water relations of four species of *Ceanothus*. M.A. thesis. San Jose State Univ., San Jose, CA.
- CARLQUIST, S. 1980. Further concepts in ecological wood anatomy, with comments on recent work in wood anatomy and evolution. *Aliso* 9:499–553.
- FERGUSON, C. W. 1959. Growth rings in woody shrubs as potential aids in archaeological interpretation. *Kivi* 25:24–28.
- . 1964. Annual rings in big sagebrush *Artemisia tridentata*. University of Arizona Press, Tucson, AZ.
- FISHBECK, K. and J. KUMMEROW. 1977. Comparative wood and leaf anatomy. Pp. 148–161 in N. J. W. Thrower and D. E. Bradbury (eds.), *Chile-California mediterranean scrub atlas. A comparative analysis*. Dowden, Hutchinson and Ross, Stroudsburg, PA.
- FRITTS, H. C. and T. W. SWETNAM. 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. *Advances in Ecological Research* 19:111–187.

- GLOCK, W. S. 1937. Principles and methods of tree-ring analysis. Carnegie Institution of Washington, Washington, DC.
- GRAY, J. T. and W. H. SCHLESINGER. 1981. Nutrient cycling in mediterranean type ecosystems. Pp. 259–285 in P. C. Miller (ed.), Resource use by chaparral and matorral. Springer-Verlag, New York, NY.
- GUNTLE, G. R. 1974. Correlation of annual growth in *Ceanothus crassifolius* Torr. and *Arctostaphylos glauca* Lindl. to annual precipitation in the San Gabriel Mountains. M.A. thesis. California State Polytechnic Univ., Pomona.
- HARLAN, A. D. S. 1977. *Arctostaphylos* species in the Santa Catalina Mountains of Arizona. Ph.D. dissertation. Univ. Arizona, Tucson.
- HEDRICK, D. W. 1951. Studies on the succession and manipulation of chamise brushlands in California. Ph.D. dissertation. Texas A&M College, College Station.
- HUBBARD, T. W. 1986. Stand age and growth dynamics in chamise chaparral. M.S. thesis. San Diego State Univ., San Diego, CA.
- KEELEY, J. E. 1975. The longevity of nonsprouting *Ceanothus*. American Midland Naturalist 93:504–507.
- . 1992. Recruitment of seedlings and vegetative sprouts in unburned chaparral. Ecology 73 (in press).
- KUMMEROW, J. 1981. Structure of roots and root systems. Pp. 269–288 in F. di Castri, D. W. Goodall, and R. L. Specht (eds.), Ecosystems of the world. 11. Mediterranean-type shrublands. Elsevier Scientific Publishing Co., New York, NY.
- , G. MONTENEGRO, and D. KRAUSE. 1981. Biomass, phenology and growth. Pp. 69–96 in P. C. Miller (ed.), Resource use by chaparral and matorral. Springer-Verlag, New York, NY.
- MICHAELSEN, J., L. HASTON, and F. W. DAVIS. 1987. 400 years of central California precipitation variability reconstructed from tree-rings. Water Resources Bulletin 23:809–818.
- MICHENER, D. C. 1981. Wood and leaf anatomy of *Keckiella* (Scrophulareaceae): ecological considerations. Aliso 10:39–57.
- MILLER, P. C. and D. K. POOLE. 1979. Patterns of water use by shrubs in southern California. Forest Science 25:84–98.
- MINNICH, R. A. 1987. Fire behavior in southern California chaparral before fire control: the Mount Wilson burns at the turn of the century. Annals of the Association of American Geographers 77:599–618.
- MONTYGIERD-LOYBA, T. and J. E. KEELEY. 1986. Demographic patterns of the shrub *Ceanothus megacarpus* chaparral in the long absence of fire. Ecology 68:211–213.
- MUNZ, P. A. 1959. A California flora. University of California Press, Los Angeles.
- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1968–1984. Climatological data annual summary—California. Vols. 72–88 (No. 13). Environmental Data and Information Service, National Climatic Data Center, Asheville, NC.
- PARSONS, D. J., P. W. RUNDEL, R. HEDLUND, and G. A. BAKER. 1981. Survival of severe drought by a non-sprouting chaparral shrub. American Journal of Botany 68:973–979.
- PATRIC, J. H. and T. L. HANES. 1964. Chaparral succession in a San Gabriel Mountain area of California. Ecology 45:353–360.
- POOLE, D. K., S. W. ROBERTS, and P. C. MILLER. 1981. Water utilization. Pages 123–149 in P. C. Miller, editor. Resource use by chaparral and matorral. Springer-Verlag, New York, NY.
- ROUGHTON, R. D. 1972. Shrub age structures on a mule deer winter range in Colorado. Ecology 53:615–625.
- SAMPSON, A. W. 1944. Plant succession and burned chaparral lands in northern California. Agricultural Experiment Station, Bulletin 685, University of California, Berkeley.
- SCHLESINGER, W. H. and D. S. GILL. 1978. Demographic studies of the chaparral

- shrub, *Ceanothus megacarpus*, in the Santa Ynez Mountains, California. *Ecology* 59:1256–1263.
- and D. S. GILL. 1980. Biomass, production, and changes in the availability of light, water, and nutrients during development of pure stands of the chaparral shrub, *Ceanothus megacarpus*, after fire. *Ecology* 61:781–789.
- SCHULMAN, E. 1947. Tree-ring hydrology in southern California. Laboratory of Tree-Ring Research, Bulletin No. 4, University of Arizona, Tucson.
- STOCKING, S. K. 1962. Some aspects of the influence of fire and sodium-calcium borate on chaparral vegetation. M.A. thesis. San Francisco State Univ., San Francisco, CA.
- STOKES, M. A. and T. L. SMILEY. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, IL.
- WATKINS, K. S. 1939. Stem anatomy of chaparral shrubs. *Botanical Gazette* 101:391–401.
- WEBBER, I. E. 1936. The woods of sclerophyllous and desert shrubs of California. *American Journal of Botany* 33:181–188.
- YOUNG, D. A. 1974. Comparative wood anatomy of *Malosma* and related genera (Anacardiaceae). *Aliso* 8:133–146.

(Received 18 Aug 1991; revision accepted 28 Jul 1992.)